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Early life expenditure in sexual competition is associated with increased reproductive senescence in male red deer

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The evolutionary theories of senescence predict that investment in reproduction in early life should come at the cost of reduced somatic maintenance, and thus earlier or more rapid senescence. There is now growing support for such trade-offs in wild vertebrates, but these exclusively come from females. Here, we test this prediction in male red deer (*Cervus elaphus*) using detailed longitudinal data collected over a 40-year field study. We show that males which had larger harems and thereby allocated more resources to reproduction during early adulthood experienced higher rates of senescence in both harem size and rut duration. Males that carried antlers with more points during early life did not show more pronounced declines in reproductive traits in later life. Overall, we demonstrate that sexual competition shapes male reproductive senescence in wild red deer populations and provide rare empirical support for the disposable soma theory of ageing in males of polygynous vertebrate species.

1. Introduction

The process of senescence is defined as a progressive deterioration of the physiological function of an organism, leading to a decline in survival or reproductive performance with age [1]. Current evolutionary theories of senescence [2–4] predict that mortality increases and fertility decreases from age at sexual maturity onwards. However, recent comparative studies have revealed that patterns of survival (i.e. actuarial) and reproductive senescence can be extremely diverse across species [5,6]. For example, actuarial senescence often starts much later than sexual maturity [5] and unexpected increase in fertility or decline in mortality with increasing age have been reported in some case studies [6]. Recently, it has been suggested that the disposable soma theory [7] might offer the best theoretical framework to explain observed variability in senescence patterns [6]. The disposable soma theory, which is grounded in the principle of energy allocation [8], posits that when an individual increases its allocation to reproduction during early life, the quantity of resources available for its maintenance over the same period will be reduced [9]. Then, the damage occurring at the tissue and cellular levels in organisms will not be efficiently repaired, which will cause later increased senescence in fitness-related traits [7,9]. Therefore, the energy trade-off between reproduction and survival, which corresponds to the core of the disposable soma theory, can also explain why in some cases mortality decreases with increasing age when energy is directed towards somatic maintenance at advanced ages [6]. Surprisingly, while long-term individual-based monitoring of animals has revealed that senescence occurs in both sexes in either captive [10] or free-ranging [11] populations, empirical tests of the disposable soma theory of ageing in natural populations have mostly focused on females [12,13] and little is known about the factors that can modulate senescence patterns in males.

In polygynous and dimorphic species, males obviously do not suffer costs associated with parental care [14]. However, they are involved in intense sexual competition to secure mating opportunities [15], leading to substantial energetic and fitness costs [16,17]. These costs have been proposed to explain why in polygynous but not in monogamous species of birds and mammals, adult life expectancy is much lower in males than in females [18,19]. However, at the individual level, the negative impacts of male expenditure in sexual competition on late life survival or reproductive performance have so far only been evidenced in laboratory settings [16,20].

Here, we use the exceptionally detailed long-term monitoring of red deer on the Isle of Rum (Scotland) to test whether male expenditure in sexual competition during early life influences reproductive senescence in late life, as predicted by the disposable soma theory. Red deer are highly polygynous and males devote a substantial amount of energy to intra-sexual competition during the autumn rut [21]. They compete intensively during this period to control harems and mate with females as soon as they enter oestrus [22], and can lose up to 35% of their body mass in the process [23,24]. Males also grow antlers anew each year, which are involved in fights during intra-sexual competition and their size is positively associated with lifetime reproductive success [25,26]. Antlers are expected to be energetically costly both to grow and maintain [27], because they constitute the only mammalian structure that is regenerated repeatedly over life and shows the fastest growth observed for an animal tissue [28]. Overall, the quantity of energy a male expends each mating season has been estimated to be around 25% of the annual energy budget [24]. Previously, we have shown in this population that females which produce more offspring during early adulthood show a steeper rate of reproductive senescence in late life [13,29]. We have also demonstrated that in males, annual reproductive success and behavioural measures associated with rutting effort (like mean harem size or rut duration) all decline rapidly from 10 years onwards, although antler size does not [30]. However, whether male red deer trade late life reproductive performance for high reproductive performance early in life remains unknown in any vertebrate species in the wild. We expected that males with an increased reproductive effort during early life should show stronger senescence in both reproductive performance and antler growth at old ages.

2. Material and methods

(a) Study population and data collection

Red deer in the North Block of the Isle of Rum, UK, have been intensively studied since the early 1970s. Individual deer are recognizable as a result of artificial markings with ear tags and natural idiosyncrasies [22]. Regular censuses of the population, daily observations during the annual rut and calving seasons, and intensive searches for dead deer during winter allow accurate estimates of birth dates, death dates and complete reproductive histories to be obtained for most deer resident in the study area [22]. During the rut (September–November), adult male deer compete to control harems and mate with females when they come into oestrus. Females older than 2 years of age give birth to a single calf between late May and June. Calves were weighed, sexed and individually marked at capture (see [22] for further details). In this study, all data available for males born after 1968 that were involved in the rut between 1972 and 2011 were included in the analyses.

Immigrant males were removed from the analyses due to their unknown date of birth.

(b) Harem size, number of days spent rutting and antlers

During the rut, daily censuses of the North Block study area were conducted to monitor male reproductive performance and female oestrus signs. The identities of females in the harem of each rutting male on each day were recorded. As in Nussey *et al.* [30], we measured the average size of a given male's harem, including days only on which the male was observed actually holding a harem across the entire rutting season. We also counted the number of days across the rutting season (from 15th September to 15th November) during which a given male was observed holding a harem of females.

Antlers are male secondary sexual traits of most deer species, which are regrown each year. Red deer grow their antlers through spring and summer for use in competitive interactions during the autumn rut. Antlers are cast during spring and are regrown, covered in a highly vascularized tissue known as 'velvet', which is shed or rubbed off during the summer months preceding the rut (known as antler 'cleaning' [30]). Regular searches for antlers through spring and summer mean that many cast antlers were recovered for measurement, and antlers were also measured from skulls recovered from carcasses during winter mortality searches. The unique shape of each antler allows the identity of the focal male to be determined. Genetic analyses of DNA extracted from antler bones indicated that recognition methods have a high success rate (93%, J. Pemberton 1998, unpublished data). Moreover, since the morphology between misidentified antlers and correctly assigned antlers will be similar, errors are expected to have a negligible impact on the following analyses. We took four measures to assess male allocation to antlers: the length (measured from the base to the farthest tip of the antler), the circumference of the coronet (measured at the base of the antler), the number of points (counted on the entire antler) and the weight (measured at the study site using an electronic top pan balance accurate to 0.1 g). Broken antlers were excluded from the analyses (following [30]). When both cast antlers were recovered (or when measures were made on an animal post mortem) mean values across both antlers were taken. Antler traits were analysed relative to male age during the rut in the previous calendar year, when antlers influenced reproductive performance.

(c) Principal component analyses

Harem size, number of days that males spent rutting, antler length, number of points on antlers, coronet circumference and antler weight all represent indices of allocation to sexual competition, which can lead to increased lifetime reproductive success in male red deer. However, these variables are likely to be positively correlated and including all of them in our models would cause problems of over-parametrization and multicollinearity [31]. Therefore, we performed a principal component analysis (PCA) on traits measured during early life (between 4 and 9 years of age) to determine their correlation structure and test whether and how we might reduce the number of traits in our analyses. We defined the early life period as up to and including 9 years of age, since previous work has shown that reproductive traits start to decrease from around 10 years of age in male red deer [30]. To remove any age effect for traits with repeated measures (such as harem size, the number of days that males spent rutting and the four antler traits) between 4 and 9 years of age, we standardized the data by centring values on the mean value of the trait for each age. Then, to keep only one value per individual for each trait over this period, we used

the mean of these standardized values. We ran PCAs on males that were known to be rutting between 15th September and 15th November of each year. Analyses were also run on a reduced dataset limited to males that survived beyond 9 years of age ($N = 109$ individuals). In addition, because some males can gain sneaky matings at the end of the rutting season, we repeated these analyses using information restricted to males rutting between 15th September and 31st October. As the results were qualitatively similar in all cases, we only report here the results obtained on the entire dataset during the whole rut period.

(d) Senescence in reproductive traits

Before testing for a trade-off between early and late life expenditure on male reproductive traits, we first looked for the best age function describing senescence in harem size and number of points on antlers during late life (from 10 to 16 years of age). We used linear mixed effect models with 'male identity' and 'year of observation' as random effects, and 'population density' and 'age at last reproduction' as covariates. The inclusion of 'age at last reproduction' allowed us to control for selective disappearance arising from individual heterogeneity [32]. We compared the fit of models without age, with age, age^2 and age^3 on the basis of the Akaike's Information Criterion (AIC). We calculated AIC weights (AICw) to assess the relative likelihood of each model to be the best among all the fitted models [33]. We selected the model with the lowest AIC. When the difference of AIC (denoted ΔAIC) of two competing models was within two units, we retained the simplest model to satisfy parsimony rules. All results from model selection are presented in the electronic supplementary material, tables S1 and S2. Results of the analyses remained unchanged when we pooled all males older than 14 years within a single age class.

(e) Early versus late life expenditure on sexual competition

To test the disposable soma theory in male red deer, we analysed how expenditure on sexual competition during early life influenced the senescence pattern in harem size and number of points on antlers during the late life period. For each of these traits, we added to the previously selected model traits that quantified the expenditure on sexual competition in early life as independent variables, both with and without interactive effects with age. We identified the model to select based on the AIC criterion (see above). In all these mixed effect models, 'male identity' and 'year of observation' were included as random effects, and 'population density' and 'age at last reproduction' were entered as covariates.

3. Results

Most of the variation in traits associated with male expenditure in sexual competition in early life (4–9 years of age) was well captured by just two measures: the mean harem size and the number of antler points. The PCA performed on traits associated with allocation to sexual competition from 155 males through early life identified two axes of variation in the covariation among traits of sexual competition. The first axis (PC1) included harem size and number of days spent rutting and can thus be interpreted as a continuum of behavioural expenditure on sexual competition, whereas the second axis (PC2) included all antler measurements, which corresponded to a continuum of antler size (electronic supplementary material, figure S1). PC1 and PC2 explained 44.57% and 22.15% of the variance, respectively. We used the circle of correlations

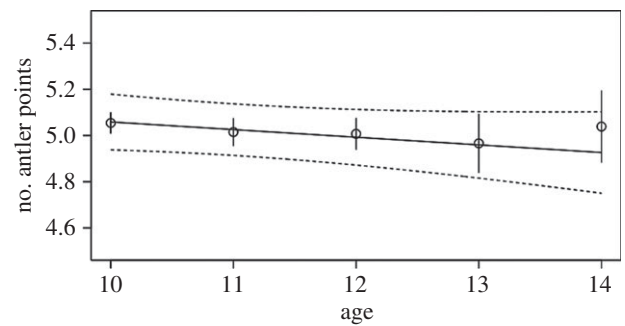


Figure 1. Relationship between the number of antler points and age from 10 years of age onwards in male red deer. All males older than 14 years are pooled with the 14 years age class. The lines represent model predictions with their 95% CIs.

Table 1. Linear Mixed Models retained to explain observed senescence in harem size from 10 years of age onwards. This model was based on 267 observations of 107 males. Variances of the random effects are 6.17 and 0.09 for 'male identity' and 'year of observation', respectively.

	harem size		
	estimate	s.e.	t
intercept	11.74	3.28	3.579
age at last reproduction	0.055	0.251	0.220
density	−0.011	0.012	−0.923
age	−0.459	0.179	−2.566*
early harem size	4.190	1.118	3.748***
age × early harem size	−0.319	0.102	−3.136**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(electronic supplementary material, figure S1) to select one measure of each component of early life allocation of males to sexual competition. Since the four antler traits were tightly linked, we only retained the number of antler points. Likewise, based on the strong relationship linking harem size and number of days spent rutting, we retained only the mean harem size. We chose mean harem size and number of antler points because these traits were measured most frequently in both early and late life. We next examined the pattern of ageing in late life (10 years onwards) in mean harem size and in the number of antler points. We found that harem size decreased linearly between 10 and 16 years of age (electronic supplementary material, figure S2 and table S1), but there was no evidence of senescence in the number of antler points (figure 1; electronic supplementary material, table S1).

Males with larger harems in early life tended to have larger harem size in later life and showed a greater rate of decline in harem size with age (figure 2), as revealed by the statistically significant effects of the interaction between age and the expenditure in harem size during early life (table 1 and electronic supplementary material, table S2). Males controlling the largest harems between 4 and 9 years of age, which were likely to expend more energy during the rut, consistently had larger harems. However, the steeper rate of decline in these traits with age led these males to have similar

Table 2. Linear Mixed Model selected to explain observed variation in the number of antler points from 10 years of age onwards. This model was based on 273 observations of 118 males. Variances of the random effects are 0.11 and 0.12 for 'male identity' and 'year of observation', respectively.

	no. antler points		
	estimate	s.e.	t
intercept	3.87	0.78	4.93
age at last reproduction	0.07	0.03	2.48*
density	0.002	0.004	0.43
early number of antler points	0.98	0.07	14.88***

* $p < 0.05$, *** $p < 0.001$.

expenditure on sexual competition as other males when reaching 13 or 14 years of age (figure 2). These results were corroborated by analyses where we replaced harem size by the number of days spent rutting as a late life trait. In these complementary investigations, we observed an association between a large harem early in life and a more rapid decline in the time spent rutting later in life (electronic supplementary material, figure S3).

We found no evidence that the number of antler points in early life had any influence on late life harem size or rut duration (table 2; see also the electronic supplementary material, table S2). Males with many antler points in early life retained more antler points in late life (table 2).

4. Discussion

Our findings support the predictions of the disposable soma theory of ageing, which predicts a negative relationship between allocation to reproduction during early life and fitness-related traits in late life [34]. We found that male red deer that control larger harems and rutted for longer periods between 4 and 9 years of age experienced stronger senescence in both of these traits between 10 and 16 years of age. This provides evidence that senescence in male reproductive traits is modulated by expenditure on sexual competition during early adulthood in a wild population of a polygynous and dimorphic mammalian species. Until now, the only evidence of a long-term cost of early reproductive effort in vertebrate males came from a captive population of Houbara bustards (*Chlamydotis undulata*) in which males with extravagant courtship behaviours showed more rapid senescence in sperm function-related traits [35].

In seasonally breeding mammals, the mass loss observed during the mating season [24,36,37] indicates that expenditure in sexual competition clearly limits males' abilities to maintain somatic condition, at least temporarily. Somatic damage accumulated over repeated high-investment ruts is one possible explanation for more rapid declines in reproductive performance during late life. Higher expenditure of resources on competition in early life could also limit energy available for somatic maintenance (e.g. immune defence against pathogens or antioxidant defence), which might result in earlier or more rapid senescence. Although no physiological traits were measured on male red deer on

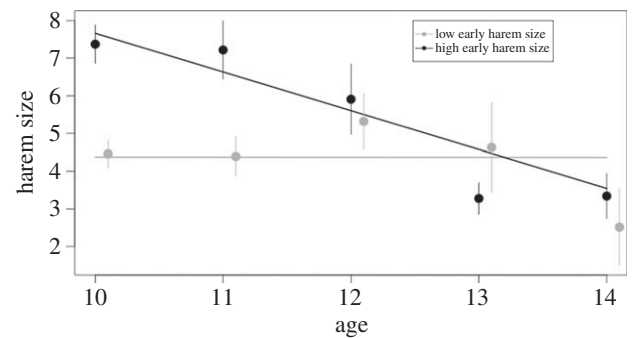


Figure 2. Relationship between harem size and age for males that allocated more (black circles, black line) or less (grey circles, grey line) than the median value of 0.055 to harem size during early life. All males older than 14 years are pooled with the 14 years age class.

the Isle of Rum, the positive trend between time spent fighting and mass loss observed in fallow deer (*Dama dama*) [36] suggests that, at least in polygynous and size dimorphic deer species, somatic deterioration might be more pronounced in males controlling relatively large harems. In addition, in vertebrates, the level of testosterone is positively correlated with male reproductive effort [38–40], notably with the ability to control large harems [41]. Therefore, males controlling large harems and rutting for long periods might suffer the most from the immunosuppressive effect of androgens [42,43], which would be in agreement with the recent finding that male red deer with high levels of plasma testosterone have high parasite loads [44]. However, despite showing steeper rate of reproductive senescence from 10 years of age, males with the largest expenditure in reproductive effort during early life controlled larger harems and rutted for longer between 10 and 13 years of age than males with the lowest expenditure in reproductive effort. This is noteworthy because the annual reproductive success of male red deer is very low beyond 13 years of age [30]. Therefore, although high reproductive expenditure in early adulthood is associated with an increased rate of decline in late life, this decline is not sufficient to negate the phenotypic superiority of these males until extreme old age. This raises the possibility that the steeper rate of reproductive senescence observed in males with the greatest reproductive effort during early life might arise from the high level of competition that these males have to face. Reproductively superior males, holding the largest harems, are likely to be under the strongest competitive pressure in the rut. Thus, declines in condition in later life could result in harem losses under intense pressure from competitors, while a similar decline in an inferior male under much lower competitive pressure might not result in any meaningful losses. Therefore, differences in the level of competition between high- and low-quality males can be responsible for the observed differences in reproductive senescence rates. However, such hypothesis does not preclude the disposable soma theory, under which differences in reproductive senescence rates should be driven by the costs associated with the level of expenditure in sexual competition during early life as an evolutionary explanation.

Our analyses failed to detect any effect of male expenditure on antlers on reproductive senescence. Males with high reproductive effort during early adult life still carried the most developed weapons at old ages. This result supports recent evidence that secondary sexual traits show contrasted

patterns of senescence across animal species (e.g. [35,45]). Moreover, it questions the long-standing idea that growing and carrying conspicuous sexual traits such as long and complex antlers is costly [46]. That red deer antlers generate only low energetic costs has been previously reported by Bobek *et al.* [24], who measured the energetic expenditure of antler growth to be only 1% of the total annual energy budget. Finally, this result is also in line with recent findings demonstrating that in mammals growing large weapons does not promote faster senescence [47] and suggests that antler size might thus be an honest signal reflecting phenotypic quality, which generalizes similar conclusions reached in roe deer (*Capreolus capreolus*) [48].

Overall, this study provides the first demonstration in the wild that a decline in reproductive performance in late life is potentially explained by the disposable soma theory in males of polygynous and dimorphic species like red deer. By comparing our results with previous reports in female red deer [13,29], we reveal for the first time that decline in reproductive performance in late life is potentially explained by the disposable soma theory in both females and males from the same species, which has important implications for the understanding of sex differences in ageing patterns. According to our current evolutionary theory of senescence, the sex with the highest mortality rate should suffer from a more rapid senescence [3]. This statement is often evoked to explain why males in mammalian populations are both more sensitive

to harsh environmental conditions [49] and suffer from higher rates of actuarial senescence than females [50]. Therefore, our results suggest that costs associated with high reproductive expenditure in males might exacerbate the sex differences in senescence patterns recently reported [18]. Finally, our results potentially fit predictions issued from the antagonistic pleiotropy of ageing which states that high reproductive energy expenditure during early life is under the influence of an allele that promotes physiological decline in late life [3]. Such a genetic basis underlying early–late life trade-offs has previously been revealed through quantitative genetic analyses in female swans [51] and female red deer [52] but has not been yet tested in males.

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Data accessibility. Data used in this paper are available in Dryad (doi:10.5061/dryad.617bk).

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